A PLIOCENE PHOCID FROM SOUTH AFRICA

By
Q. B. Hendey

South African Museum, Cape Town

&

Charles A. Repenning

U.S. Geological Survey, Menlo Park, California

(With plates 2–18, 2 figures and 7 tables)

[*MS. accepted* 9 *September* 1971]

Contents

Introduction

Although Illiger recognized the basic features of the seals of the world in 1811 by separating them from the sirenians and placing them in a separate order, the Pinnipedia, their classification is still in a state of flux. In 1880 Allen divided the pinnipeds into two major groups: the 'walkers' and the 'wrigglers' which Smirnov (1908) subsequently named the superfamilies Otarioidea and the Phocoidea. The Phocoidea contains only one family, the Phocidae (Gray 1825, but defined with its present contents by Brookes, 1828), usually known as the 'earless seals' or 'true seals'. Subsequent to Kellogg's (1922) introduction of the subfamily Lobodoninae (respelled Lobodontinae by Hay, 1930) to include the Antarctic phocids, the family Phocidae was considered to include four subfamilies: Phocinae for the northern seals, Monachinae for the genus *Monachus*, Cystophorinae for the genera *Cystophora* and *Mirounga*, and Lobodontinae. Scheffer (1958) reduced the rank of the Antarctic phocids to that of a tribe, Lobodontini, within the family Monachinae. King (1966), in possibly one of the most detailed explanations of a change in pinniped classification, abandoned the subfamily Cystophorinae, placing the genus *Cystophora* in the Phocinae and the genus *Mirounga* in the Monachinae. Most recently (at this writing) McKenna

Ann. S. Afr. Mus. **59** (4), 1972: 71–98, 17 pls, 2 figs, 7 tables.

(1969), in possibly one of the briefest explanations of a change in pinniped classification, stated that the formal taxon order Pinnipedia has been abandoned.

As here used, the order Pinnipedia contains three families: Odobenidae, the walruses; Otariidae, the sealions; and Phocidae, the true seals who must 'wriggle' on their bellies in terrestrial locomotion, their hind limbs permanently extended behind them. The family Phocidae contains two distinct subfamilies, the Phocinae, inhabiting temperate and arctic waters of the Northern Hemisphere, and the Monachinae, inhabiting parts of most oceans except the Arctic Ocean.

For the most part, the characters identified by King (1966) may be used to separate the living members of the two phocid subfamilies. Since it is assumed that the two subfamilies derive from a common ancestor, it is to be expected that fewer of these characters will be useful for familial identification in the fossil ancestors of the living true seals. Such is the case with the Pliocene phocid from South Africa.

Since 1958, when the first discoveries from the quarries of the African Metals Corporation were recorded by Singer & Hooijer (1958), tens of thousands of vertebrate specimens have been recovered from these Pliocene phosphate deposits near Langebaanweg, Cape Province. At least 60 mammalian species, as well as a full complement of birds and cold-blooded vertebrates, have been recognized (Hendey, 1970*a*, 1970*b*). The fauna is both marine and terrestrial, apparently representing accumulation during a prolonged period of marine, estuarine, and terrestrial deposition in the area.

The dating of the Langebaanweg fauna is a major problem presently being investigated (Hendey, 1970*b*; Maglio & Hendey, 1970). On the basis of an admittedly limited number of comparisons with faunal elements from better-dated localities in East Africa, we believe the Langebaanweg deposits bearing the main body of higher vertebrate remains to be perhaps 4 to 5 million years old. The most recent interpretation of the most reasonable definition of Pleistocene, and the approximation of its beginning between 2,6 to 3 million years ago (Savage & Curtis, 1970), suggest that the Langebaanweg fauna should probably be called late Pliocene.

The Langebaanweg fauna includes a pinniped which was first reported by Boné & Singer (1965). These authors tentatively referred it to the otariid genus *Arctocephalus*, but more recently discovered specimens show clearly that it is a monachine phocid which belongs to a previously unrecorded species of the extinct genus *Prionodelphis*, heretofore known only from Pliocene deposits in Argentina. In many respects this seal from Langebaanweg is similar to the extant *Monachus* and its ancestors, notably *Pliophoca etrusca* from the late Pliocene of Italy (Tavani, 1942). However, similarities to the extant phocids of the Antarctic seas are equally well marked.

In view of the small number of recorded specimens of *Prionodelphis rovereti* (Frenguelli, 1922, 1926), from Argentina, the Langebaanweg seal, represented by a wide variety of specimens, is clearly important in that it provides the first good evidence of the antiquity and ancestry of the monachine seals in the Southern Hemisphere.

Systematics

As here used, the subfamily Monachinae includes the same genera of living seals that were included in this subfamily by King (1966). Except for the addition of the genus *Mirounga*, this agrees with the definition of the subfamily as originally defined by Trouessart (1897:373).

As noted by Scheffer (1958:111), when he reduced the Lobodontinae to tribal rank within the Monachinae, the major difference between these Antarctic seals and *Monachus* is one of geography. King (1966) omitted reference to Scheffer's tribe Lobodontini when discussing the monachine relationship of *Mirounga*, with good reason as the genus does not conform to the geographic distinction mentioned by Scheffer. Recognition of any tribal subdivision of the Monachinae now seems pointless.

King (1966:397) noted that with some features otherwise typical of the monachine seals *Monachus* was an exception and regarded this genus as being not quite so advanced. Such exceptions to otherwise typical features of the Monachinae are even more evident in the Pliocene seal from Langebaanweg. At this stage in the evolution of the phocid seals the subfamily Monachinae can be distinguished from the subfamily Phocinae by the following characters of the skull.

Subfamily **Monachinae**

Diagnosis. Seals having a mastoid bone without a prominent posterolaterally projecting rounded crest but, instead, having a posterolateral surface curving uniformly from the region of the parietal suture down to the region of the stylomastoid foramen; mandible with an extensive symphyseal surface that is elongate and smoothly oval in outline and that firmly articulates over the entire depth of the chin.

As will be shown in the following report, some postcranial bones of the Langebaanweg seal exhibit monachine features while other are simply phocid, with no subfamilial characteristics.

Genus *Prionodelphis*

Type. Prionodelphis rovereti Frenguelli, 1922.

Known distribution. Pliocene of the South Atlantic Ocean.

Comment. The type species, *Prionodelphis rovereti*, was described as a squalodont cetacean from a few isolated teeth found in Pliocene deposits in Entre Rios in Argentina. A mandibular fragment bearing one tooth was later found at the same locality which led Cabrera (1926:390) to the conclusion that the animal was a pinniped, a conclusion supported by others (Frenguelli, 1926;

Kraglievich, 1934; Kellogg, 1942). We are aware of no additional material.

The material from South Africa now makes it possible to provide a better definition of the genus.

Diagnosis. A generalized monachine seal lacking the shortened rostrum and crowded teeth of *Monachus monachus* and the squared premaxillaries with aligned, upper incisors of *M. tropicalis* and *M. schauinslandi*; postcanine teeth low-cusped as in *M. schauinslandi*, *M. tropicalis* and *Pliophoca etrusca* and distinctly narrower in occlusal outline than those of *M. monachus*; upper fifth postcanine[1] with recurved crown; ascending ramus of premaxilla strong, terminating against nasals and prominently visible in lateral view separating maxilla from nasal aperture; pre-orbital processes prominent; forehead broad in supra-orbital region; osseous nasal septum strongly developed; dental formula 2.1.5/2.1.5; tympanic bulla covers petrosum.

THE LANGEBAANWEG SEAL

Prionodelphis capensis n.sp.

Holotype. An incomplete skull with left canine and fourth postcanine, and right third postcanine (South African Museum No. L 15695).

Referred material. An incomplete skull (L 12695); temporal bone (L 15652); mandible fragments (L 7556, L 12299); one lower and two upper incisors; three lower and four upper canines; and nine lower and ten upper postcanines.

Various elements of the postcranial skeleton have been recovered, of which the following have been selected for description: vertebrae (L 7563, L 15689, L 15849A1 & A2, L 15396, L 15857); scapula (L 2160); humeri (L 2157, L 4638); ulnae (L 2161, L 15682); radii (L 2935, L 12869), innominate (L 15849A), femur (L 10131); tibiae (L 2138, L 10128/9); calcaneum (L10118); astragali (L 10130, L 10993); navicular (L 15851); entocuneiform (L 10134); metapodial (L 10996); first phalanx (L 10999); second phalanx (L 10205).

All specimens are housed in the South African Museum, Cape Town. Except for the two incomplete skulls, which are too fragile to cast, casts of the more significant specimens are housed in the U.S. Geological Survey, Pacific Coast Center, Menlo Park, California.

Locality and horizon. The holotype and most of the referred material is from horizon 2, 'E' Quarry, Langebaanweg. Some postcranial elements are known from horizon 1. These horizons are thought to be broadly contemporaneous (Hendey, 1970*b*). A few fragmentary remains from 'C' and Baard's Quarries are excluded from this report, but they apparently represent the same species.

Comparative material. Skulls of all living phocid species except *Pusa caspica* have been available for comparison either in the South African Museum or in the Pacific Coast Center of the U.S. Geological Survey. Postcranial material has been somewhat less available, but comparisons were made with postcranial

---

[1] Called P_1 by Frenguelli, 1922: 496.

elements of *Monachus schauinslandi*, *Hydrurga leptonyx*, *Lobodon carcinophagus*, *Mirounga angustirostris*, *M. leonina*, and all living phocine genera.

Diagnosis. *Prionodelphis capensis* differs from the type species in that it has only one anterior accessory cusp on the lower postcanines instead of two, and there is a greater reduction in size of the posterior root in the second to fourth upper postcanines. The cheek-teeth of the South African species approach more closely a three-cusped tooth pattern, and in addition, are slightly larger and more laterally compressed (Table 1).

TABLE 1. Average length-width ratios for postcanines 2 to 4 of some phocids.

	Length	Width	W/L × 100	Upper/ Lower
Hydrurga leptonyx				
Upper (N = 6)	18, 0 mm	8,8 mm	49	0,925
Lower (N = 6)	17,6	9,3	53	
Prionodelphis capensis				
Upper (N = 7)	13,8	7,5	54	1,200
Lower (N = 8)	15,0	6,8	45	
Prionodelphis rovereti[1]				
Upper (N = 1)	12,25	8,0	65	1,204
Lower (N = 2)	13,0	7,0	54	
Monachus schauinslandi				
Upper (N = 6)	12,0	7,9	66	1,047
Lower (N = 6)	12,1	7,6	63	
Monachus monachus				
Upper (N = 6)	12,9	9,1	70	1,111
Lower (N = 6)	12,9	8,0	63	

[1] From Frenguelli, 1922.

DESCRIPTION

The assessment of the fossil remains listed above is somewhat hampered by their fragmentary nature. The holotype is composed of about 60 individual pieces, including three teeth, found scattered over a wide area in the excavation No. LBW 1969/1 (South African Museum departmental records). Numerous small pieces could not be restored to the skull, although they undoubtedly belong, and others presumably remain in unexcavated parts of the deposit.

The second partial skull (L 12695) was similarly fragmented. Although the partially restored snout region is less complete than that of L 15695, parts of the braincase of the second specimen were also recovered. Many of the individual pieces are extensively abraded, probably having suffered in a manner similar to that described for an alcelaphine skull recovered near by (Hendey, 1970*a*: 82).

As with much of the referred material, the temporal bone (L15652) also came from the excavation LBW 1969/1, but from approximately 75 cm below the holotype. It probably belongs to another individual.

Most of the isolated teeth were recovered intact, and they vary from unworn to extremely worn.

Few elements of the postcranial skeleton were recovered intact, but in some cases sufficient numbers of a particular bone are known to enable a complete assessment of its characteristics.

THE SKULL

The skull of the Langebaanweg pinniped is in many ways unique, and it exhibits a set of characteristics which makes it impossible to assign it to any previously known phocid species (Plates 2–8).

As a whole, the skull appears convincingly to be that of a monachine seal. The lack of swollen or crested mastoids, the broad and flat dorsal surface of the petrosal apex, and the deep and oval mandibular symphysis rule out any known phocine seal, while the incisor formula and cheek-tooth pattern strongly suggest a monachine seal. Although the postcranial bones in general also appear monachine, they possess some features that are characteristic of living phocine seals, such as an entepicondylar foramen on the humerus.

In general features, the skull most resembles those of *Monachus* and *Hydrurga*, although it is considerably more gracile and less elongated than the latter. Of all extant genera its teeth most resemble those of *Monachus*. However, except for the lack of great vertical exaggeration of the cusps, the teeth are also quite similar to those of *Hydrurga*. Of the extinct genera they are, as far as comparisons are possible, most similar to *Prionodelphis rovereti* and, less so, to *Pliophoca etrusca*. The basic pattern of the cheek-teeth appears to be that of earlier members of the family Phocidae.

Unlike the usual pattern in the Antarctic monachines, the premaxilla terminates against the nasal bone. Although it shares this characteristic with *Monachus* and several phocine seals, it differs markedly, as does *Pliophoca etrusca*, in the massiveness of the ascending ramus of the premaxilla. When the

TABLE 2. Dimensions of the skull of *Prionodelphis capensis* from Langebaanweg.

	L15695	L12695	L7556	L12299
Rostral width	48,0*	61,0*	—	—
Distance between pre-orbital processes of maxilla . . .	94,0*	—	—	—
Minimum diameter of inter-orbital region	36,0*	—	—	—
Distance between pre-maxillary projections and posterior limit of nasal aperture	58,0*	51,0*	—	—
Lengths of nasals.	62,0*	—	—	—
Distance between external alveolar margins of fifth postcanines . .	74,5*	87,0*	—	—
Alveolar length of upper postcanine series	72,5	72,5*	—	—
Alveolar length of lower postcanine series	—	—	66,5	—
Depth of mandible behind M_1 . .	—	—	27,9	31,6

* Estimated.

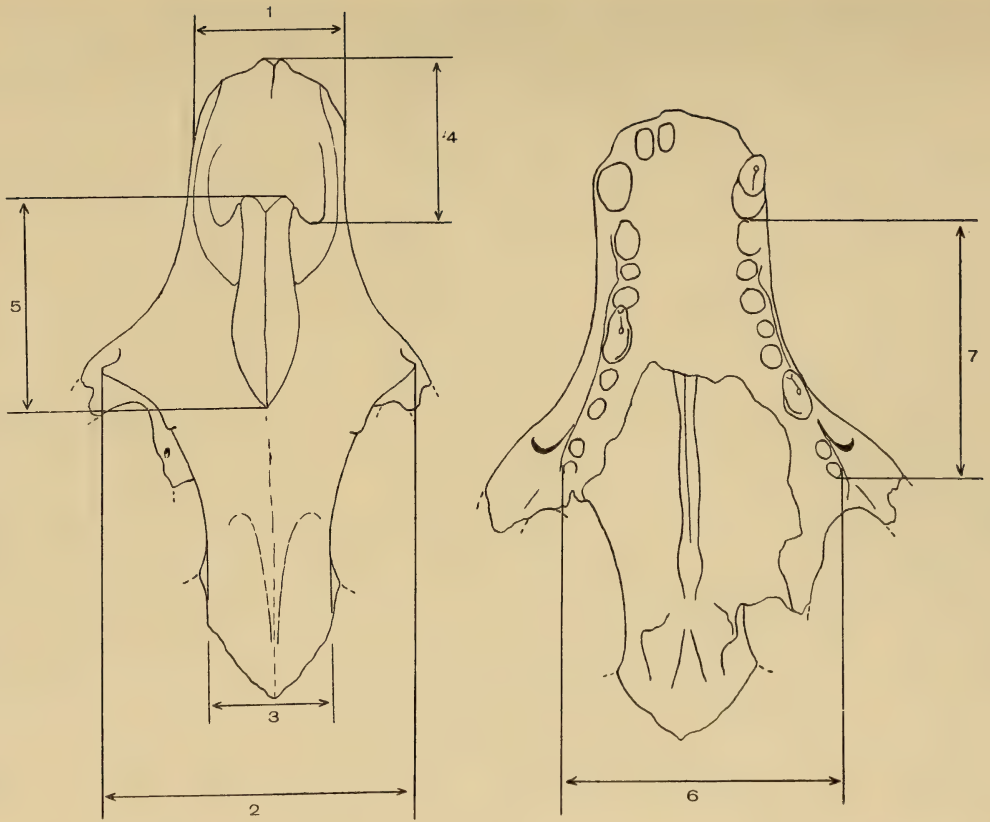

Fig. 1. Diagram of cranial measurements: 1. Rostral width. 2. Distance between pre-orbital processes of maxilla. 3. Minimum diameter of inter-orbital region. 4. Distance between premaxillary projections and posterior limit of nasal aperture. 5. Length of nasals. 6. Distance between external alveolar margins of fifth postcanines. 7. Alveolar length of upper postcanine series.

skull is viewed laterally the premaxilla is visible along its entire length rather than being partly hidden behind the maxilla, largely within the nasal opening, as in living monachines. The nasal opening is elongated antero-posteriorly, and of the southern phocids most resembles *Hydrurga* and *Lobodon*, rather than *Leptonychotes* and *Ommatophoca* in which there is foreshortening of the anterior part of the snout. In this respect it is also similar to *Monachus* and *Pliophoca.* The two halves of the premaxilla have fairly prominent projections at their most anterior point of contact, dorsal to the incisors. Of the extant monachines *M. tropicalis*, *M. schauinslandi* and *Hydrurga* have similar projections, but in *Hydrurga* inflation of the alveolar region of the incisors renders the projections less prominent, and in the two *Monachus* species the projections are quite widely separated. In the fossil species there is a marked step between the most anterior maxilla-premaxilla contact and the premaxillary projection. This is best seen in the specimen L 12695.

Judging from the size of the alveoli, the lateral incisor is only slightly larger than the medial one. The latter is situated slightly anterior to the other. The relative size and position of the upper incisors are as in *M. monachus* and *Hydrurga*, and unlike the specialized condition found in *Lobodon* and *Leptonychotes*, in which genera the lateral incisor is much larger than the medial one and is situated in line with it.

Two upper incisors are known, both left medials judging from their size. The structure of the crown resembles that of the incisors of *M. monachus* and *Pliophoca etrusca.* The cross-section of the canines is only slightly elongated antero-posteriorly, and in this respect *P. capensis* differs markedly from the Antarctic phocids. The canines L 11686 (Plate 9B) and L 12695 have large bulbous roots, a feature also seen in some of the postcanines. This is a characteristic of old age in most or all pinnipeds.

There are five upper postcanines and at least one specimen of each dental category is known from the assemblage. The first, and smallest, is single rooted (Plate 9C). The remainder are all double rooted, with the posterior root being larger than the anterior one in the second, third, and fourth teeth, and the sizes reversed in the fifth. The latter is also the second smallest of the teeth and is set slightly separate from the others immediately below the infra-orbital foramen. The postcanine tooth rows curve outwards posteriorly as in *Ommatophoca*, and are not diverging straight lines as in *Leptonychotes* and *Hydrurga;* this pattern is rather close to that of *M. schauinslandi* as well as some other phocid species.

The postcanines resemble those of *Pliophoca etrusca*, although narrower and more gracile, and except for being much less massive, they are also similar to those of *M. monachus* (Plate 9D). They are quite distinct from the highly specialized teeth of extant Antarctic phocids; of this group the teeth of *Leptonychotes* are closest to the fossils, but they are nevertheless significantly different. The basic pattern of the first to fourth postcanines is similar to the corresponding teeth of *M. monachus*. There is a prominent central cusp with two smaller cusps situated anteriorly and posteriorly, with an additional small projection on the most posterior part of the cingulum. The enamel is generally rugose, a condition which is found in all monachine seals except *Mirounga*, but which is also found in some phocine seals. The second, third and fourth upper postcanines have a marked inflation of the postero-internal cingular region, a condition also evident in some teeth of *P. rovereti*, and *P. etrusca*, and these teeth are broader posteriorly than they are anteriorly. The first upper postcanine has the internal cingulum inflated, and the maximum transverse diameter is at about the mid-point of the tooth. The upper postcanine of *P. rovereti* described by Frenguelli (1922:493 and figs. 1b, 1c) is shorter and relatively broader than those of *P. capensis*. It lacks the distinct anterior accessory cusp present in the latter species and has a larger posterior root.

The fifth postcanine of *P. capensis* lacks the posterior accessory cusp and cingular projection, and the anterior accessory cusp is much reduced, being barely discernible; the principal cusp is strongly recurved (Plate 9E). It resembles the cheek teeth of *Leptonychotes* in this respect. Both the fifth postcanines recovered to date are completely unworn, and it seems probable that this tooth did not occlude with the lower fifth postcanine. *Leptonychotes* also has a non-occluding upper fifth postcanine. This tooth, in *P. capensis*, is very similar to one of the original *P. rovereti* specimens illustrated (as a P_1) by Frenguelli (1922: fig. 2A). The principal differences are in the smaller size of the *P. rovereti* specimen, in that its anterior accessory cusp is situated higher up the crown, and also in that there is no cingulum on the buccal surface of the Langebaanweg specimens. The two *P. capensis* specimens differ from one another only in that one is slightly shorter and somewhat broader than the other. In the postcanines such differences distinguish upper from lower teeth, but judging from the size of alveoli in mandibles and maxillae known, these teeth can only be upper fifth postcanines.

Of the seven second, third and fourth upper postcanines known, two are unworn and five show wear angled from the principal cusp to the posterior cingulum.

The general features of the maxilla of *P. capensis* correspond most closely to those of *Hydrurga*. The fossil seal has very prominent preorbital processes. The one preserved in the holotype projects outwards and downwards as in *Hydrurga*, although in L 12695 it has an outwards and upwards inflection. The presence and form of the preorbital process is variable throughout the Pinnipedia, but within the monachine seals it is virtually absent in *M. schauinslandi*, *M. tropicalis* and *Leptonychotes* and present but variably developed in other extant monachine species.

In the Antarctic phocids the jugal terminates lateral to the infra-orbital foramen, whereas in *P. capensis*, *P. etrusca*, *Monachus* and several other seals it terminates above this foramen.

The infra-orbital foramen is oval shaped as in *Hydrurga* and *Lobodon*, but the orientation of the longitudinal axis of the foramen differs in that it is directed upwards and outwards in *P. capensis*, whereas the axis is upwards and inwards in *Hydrurga* and *Lobodon*.

The shape of the nasals is not perfectly known, but from a reconstruction of this region in the holotype (Plate 2), it appears that they do not correspond in shape to those of other monachines. Instead they are broader in the frontal region than between the maxillae.

The osseous nasal septum is a very stout bone which terminates at or near the most anterior limit of the nasals. Its proportions resemble those of *M. schauinslandi*, *M. tropicalis*, *Hydrurga*, *Ommatophoca* and *Mirounga*, but not *M. monachus*, *Lobodon* and *Leptonychotes*.

The supra- and post-orbital regions of the frontal bones are essentially similar to those of *Hydrurga*, *Lobodon* and *Ommatophoca*, and are not parallel-sided as in *Monachus*, *Leptonychotes* and *Mirounga*, nor as in *P. etrusca*. In the holotype there are the beginnings of a sagittal crest towards the posterior part of the frontals. There are two step-like projections on the frontals above and behind the preorbital processes of the maxilla. Similar features are present in *Ommatophoca* and are less distinctly represented in *Hydrurga*.

The second partial skull (L 12695) belongs to an aged individual and is somewhat more robust than that of the holotype (Plate 5). The difference in size of the two specimens may in part be due to the ages of the individuals concerned, but may also reflect sexual dimorphism in the species. Apart from size, the most striking difference between the two specimens is in the form of the nasal aperture. That of L 12695 is actually slightly shorter than that of L 15695, although it is, as would be expected, wider and higher. A similar and probably related allometric feature is the correspondence in the length of the postcanine tooth rows.

The braincase of *P. capensis* is not known, although parts of the nuchal region of L 12695 were recovered. The nuchal crest is fairly well developed, being more similar to that of *Hydrurga* than other species, although, like the sagittal crest, it is considerably less prominent than that of *Hydrurga*. Unlike *Hydrurga* there is no marked concavity of the supra-occipital. As in the Antarctic seals, *Monachus monachus*, and *Pliophoca etrusca*, the nuchal crest extends anteriorly across the temporal, terminating near the external acoustic meatus, rather than uniting with an enlarged jugular process of the exoccipital as in *M. schauinslandi* and *M. tropicalis*.

The basi-cranium is largely unknown, but a number of specimens of the well-ossified temporal bone have been recovered. The most complete (L 15652) has the mastoid and most of the tympanic intact, and the post-glenoid process is still attached (Plate 6). That part of the ectotympanic which projects under the acoustic meatus has been broken off and lost.

Although the general appearance of the tympanic region is most reminiscent of *Monachus* because of the slight inflation of the bulla, some of its features strongly indicate a relationship between *Prionodelphis capensis* and the Antarctic phocids. These include the posterior extent of the bulla and the rounded apex of the petrosum.

As noted by King (1966:387), the posterior wall of the bulla in phocine seals (except some individuals of *Erignathus*), and in species of *Monachus*, is located rather far forward so that the posterior part of the petrosum is exposed in ventral aspect (without recourse to peering through the posterior lacerate foramen), whereas in the Antarctic monachine seals, including *Mirounga*, the bulla covers the petrosum and essentially separates the mastoid from the posterior lacerate foramen by almost contacting the exoccipital. The latter condition is very evident in *P. capensis*, strongly suggesting an affinity with the Antarctic seals.

The dorsal (cerebellar) surface of the temporal resembles that in some living Antarctic seals (Plate 7). The apex of the petrosum is broad and rounded with low relief, as in *Lobodon* and *Leptonychotes*, and differs greatly from the pointed apex found in *Monachus*. It is not the globular structure typical of the phocine seals. However, the petrosal apex of *P. capensis* is smaller than in the living Antarctic seals, suggesting that this seal was less well adapted for directional underwater hearing, according to the interpretation of Repenning (in press). The cerebellar fossa is relatively large, as in *Leptonychotes*, and as in the latter, the squamosal extends medially to the edge of the cerebellar fossa and to the internal facial canal.

The ventral (external) side of the temporal most resembles that in *Hydrurga*. The external opening of the carotid canal is located well forward of the posterior limit of the bulla, as in *Hydrurga*, *Leptonychotes* and *Lobodon*, but in contrast to the more posterior location in *Ommatophoca*, *Mirounga* and *Monachus*. In *P. capensis* this foramen faces noticeably ventrally, as in *Hydrurga*, but the general outline of the bulla is more similar to that in *Lobodon*. The stylomastoid foramen is rather widely separated from the external cochlear foramen (Burns & Fay, 1970:374). A similarly wide separation is found in *Hydrurga*.

Dissection of the middle ear was not undertaken.

The mandible is rather unspecialized and resembles that of *Hydrurga* and *Monachus* (Plate 8). It differs from that of *Hydrurga* in its smaller size and in having the symphyseal region relatively narrower transversely. In *Hydrurga* the two lower incisors are situated side by side, but in the fossil the medial incisor lies in an almost horizontal position above and behind the lateral incisor, in a manner comparable to that in most other species of phocid seals.

A single isolated lower medial incisor (L 15444A) is known. It is similar in size to that of *Leptonychotes* but has a pronounced step on the lingual surface of the crown which, in lateral view, resembles that of *Monachus*.

The lower canines are similar to the uppers, but have a straighter root and are more rounded in cross section.

The five lower postcanine teeth are situated close to one another: the alveolar walls between the teeth are as narrow as, or narrower than, those between the two roots of one tooth. In the mandibular ramus L 7556, the teeth are positioned in much the same way as in the *P. etrusca* specimen described by Tavani (1943: fig. 6a). The first postcanine is single rooted, and the remainder, which are more or less equal in size, have two roots. These teeth apparently all have a crown pattern similar to the first to fourth upper postcanines (Plate 9G). Nine isolated lower postcanines are known, one of which is identified as a first lower and two are thought to be second lowers. Both the latter are worn on their posterior surfaces. Of the remainder, three show most wear on their anterior surfaces, and four, including the first lower, show no perceptible wear at all. Judging from the wear on the upper and lower postcanines, it appears that they functioned as crushing agents, although two of the lower teeth show signs of a transverse shearing action.

The lower teeth are differentiated from the uppers by the fact that they are more slender, with little or no inflation of their internal cingula. The lower postcanines of *P. rovereti* (Frenguelli, 1922:499, figs. 2B, 2C) are shorter and relatively broader than those of *P. capensis*, and have a variably developed second anterior accessory cusp which is not present in the Langebaanweg species.

TABLE 3. Dimensions of the teeth of *Prionodelphis capensis* from Langebaanweg.

	UPPER				LOWER		
	No.	A–P diameter	Transverse diameter		No.	A–P diameter	Transverse diameter
Incisors				Incisors			
Med.	L 11689	6,1	5,3	Med.	L 15444A	3,8	3,2
Med.	L 15381B	6,3	5,2				
Canines	L 11686	10,1	7,5	Canines	L 15437	9,2	7,4
	L 15241	c. 10,2	7,5		L 15743	9,0	7,3
	L 15630B/2	c. 10,1	c. 8,0		L 13152	9,6	7,8
	L 15695	10,1	7,4				
Post-canines				Post-canines			
1st	L 11687	9,0	6,1	1st	L 15580	9,7	5,6
2nd	L 15611	13,9	c. 7,0	2nd	L 15680B/2	14,5	6,4
				?2nd	L 15736A	14,2	6,5
3rd	L 15695	14,5	7,5				
4th	L 15695	13,4	7,4				
5th	L 12562	9,8	6,4				
5th	L 15429	10,4	5,5				
?	L 12557	12,9	8,1	?	L 15429/1	c. 15,0	6,5
?	L 12556	13,7	7,8	?	L 15413B	15,4	6,4
?	L 15630B/2	13,8	7,2	?	L 10160	14,8	7,2
?	L 15664	14,1	7,8	?	L 15444B	15,2	7,0
				?	L 15771	15,0	7,1
				?	L 12124	16,0	7,3

The proportions of the upper and lower cheek teeth to one another are similar in *P. capensis* and *P. rovereti*, and differ from some extant monachines (Table 1).

The height of the mandibular corpus is fairly constant between the posterior limit of the symphysis and the fifth postcanine (Plate 8). In the mandible fragment L 12299, the masseteric fossa begins about 20 mm behind the fifth postcanine, and the ascending ramus begins inclining at about this point. There is no corresponding upward inflection of the inferior margin of the corpus as there is in *Leptonychotes*, and the fossil resembles most other phocid species in this respect.

The symphysis of the mandible is short relative to that of some monachine seals, and terminates below the posterior root of the second postcanine. It is typically monachine, however, and has a strong, oval articular surface over the entire depth of the jaw. The mandibular condyle is not known.

There are multiple mental foramina towards the anterior part of the corpus.

THE POSTCRANIAL SKELETON

While the skull characters of *Prionodelphis capensis* show its relationships to lie with the Monachinae, certain features of the postcranial skeleton are more commonly found among the Phocinae (see King, 1966). Presumably, the 'phocine' characteristics are inherited from the primitive ancestral stock, and are features which were lost by the Monachinae during their later development. Characteristics which are typically monachine are also evident.

Vertebrae

Associated with the innominate to be described later (L 15849), were a number of vertebrae, most of which were badly crushed and incomplete. However, two lumbar (L 15849A1 and A2) and one caudal vertebra (L 15857) were reasonably well preserved although still incomplete (Plate 10C, D, F). Other vertebrae recorded are an axis (L 7563), one other cervical (L 15689), and a sacral (L 15396) (Plate 10B, E), all of which are damaged, and a number of other fragmentary specimens.

Only the centrum of the second cervical vertebra is preserved. The odontoid process is prominent, with a length of 16 mm and a maximum transverse diameter of 17,7 mm. The total length of the centrum is 53 mm, and the transverse diameter of the anterior articular end is estimated to be about 55 mm. The other cervical vertebra, probably a fourth, consists of the centrum, parts of the left transverse processes enclosing the vertebrarterial canal, and part of the left half of the neural arch. The centrum is 47,6 mm long and the transverse diameter of the anterior epiphysis is 31,4 mm. Both these specimens have the reduced transverse processes which characterize the Phocidae (King, 1964:98).

The two lumbar vertebrae, a second or third and a fifth, are similar in size to those of *Pliophoca etrusca* (see Ugolini, 1902, and Table 4). The transverse processes of the fifth lumbar vertebra are very prominent, which is characteristic of all Phocidae (King, 1964:99).

Although the sacral vertebra, a third, is from an adult individual it was not fused to the second. However, the anterior end of the preserved right transverse process is markedly rugose, suggesting that there was a strong cartilaginous

TABLE 4. Dimensions of lumbar vertebrae of *Prionodelphis* and *Pliophoca*.

	Prionodelphis capensis		*Pliophoca etrusca*		
	2nd or 3rd	5th	2nd	3rd	5th
Length of centrum	60,4	55,4	62,0	61,5	55,5
Transverse diameter of anterior epiphysis	41,0	42,2	41,0	40,0	44,0

attachment between it and the posterior end of the second sacral transverse process. This specimen is unusual in that it lacks the left transverse process, and the anterior end of the centrum and neural arch are, as a result, asymmetrical with the dorso-ventral median axis directed from right to left at a slight angle to the normal line. The length of the centrum is estimated to be 38 mm, while that of a *Pliophoca etrusca* specimen is 36 mm (Ugolini, 1902).

In the caudal vertebra, a first, much of the centrum is lost, apparently having been gnawed away. Crushing, punctures, and gnaw-marks resulting from grasping and chewing by carnivores are a not uncommon feature of the fossils from Langebaanweg. Both anterior and posterior zygapophyses of the caudal vertebra are well developed, and the distance between their anterior and posterior limits is 47 mm. The transverse diameter of the anterior epiphysis of the centrum is approximately 25 mm.

Anterior Limb

Scapula

A single incomplete pinniped scapula (L 2160) is known from Langebaanweg (Plate 10A). This specimen consists of the articular end, neck and lower parts of the blade. The acromion and internal margin of the articulation are damaged.

The glenoid cavity is markedly elongated and concave; the concavity as well as the breadth/length ratio being comparable only to that of *Lobodon* and *Monachus* (67,9% for L 2160, 72,0% for one *Lobodon* scapula, and 67,1% for one *Monachus schauinslandi* scapula). Other monachine genera have shallower and more nearly equidimensional scapular glenoid fossae.

Also most comparable to *Lobodon* and particularly *Monachus*, the neck of the fossil scapula is extremely short and has an antero-posterior diameter of 45,8 mm. The spine is strongly developed for a monachine seal, but might not exceed the development of that of *Lobodon*. Too little is preserved to be certain. The sharp scapular notch, where the anterior margin of the coracoid process turns into the inferior border of the supraspinous fossa, suggests that the anterior border of the scapula may have been straight and vertical as in the Antarctic monachines.

The medial surface of the subscapular fossa is divided into two parts by a prominent ridge most resembling that of *Monachus* in its prominence and location. The ridge is more prominent than in *Monachus*, however, and is better developed than in any living phocid. Although the scapula differs greatly in other respects, the prominence of this subscapular ridge is equalled only by the

Miocene *Phoca vindobonensis* Toula (1897: pl. 9, fig. 15a).

Humerus

All fourteen humeri recovered to date in which the distal end is preserved have an entepicondylar foramen. The supinator ridge is well developed in all specimens (Plate 11). These features are characteristic of the extant Phocinae (King, 1966), but in at least one extinct monachine, *Monotherium*, an entepicondylar foramen was present (see Van Beneden, 1877). This is a characteristic of particular significance in the interpretation of the relationships of *Prionodelphis capensis*.

Because of the rather startling phocine appearance of the humerus of *P. capensis*, it is appropriate to examine this bone in greater detail. Plate 12 shows the right humeri of *Monachus schauinslandi*, *P. capensis* and *Cystophora cristata*. The humerus of *Cystophora* was selected because it, of all phocine genera, most resembles that of the fossil. The humerus of another phocine, *Erignathus barbatus*, is shown with those of *P. capensis* and *M. schauinslandi* in Figure 2. It is immediately evident that the *P. capensis* humerus exhibits not only phocine, but also monachine characteristics.

Apart from the two characters already mentioned, there is also a considerable difference between phocine and monachine humeri in the region of the deltoid crest. In all pinnipeds the pectoralis muscle is prominent, and its insertion on the humerus is strengthened. In the phocine seals this has been accomplished by an anteriorly directed enlargement of the medial edge of the deltoid crest toward the enlarged lesser tubercle, so that the intertubercular groove becomes circular in cross-section, coming to within 40° of completely encircling the bicipital tendon in some species. In the otarioid seals, the pectoral insertion is similarly strengthened in this area, and the intertubercular groove becomes trenchant, although the lesser tubercle remains 'lesser'. Strengthening of the pectorial insertion on the phocine humerus does not take place by extending the insertional area distally along the shaft of the humerus but, rather, the insertional area terminates abruptly at a strong process on the distal end of the deltoid crest. Beyond this point the anterior margin of the phocine humerus shaft is concave as it curves to meet the distal articulation, and is devoid of muscle scars.

The transverse development of the deltoid crest of phocine humeri is also in evidence laterally, where a lip of bone overhangs the area of insertion of the deltoid muscle.

In the monachine seals anterior enlargement of the deltoid crest is minimal, the intertubercular groove remains widely open, and there is no overhanging of bone on the lateral edge of the crest. The pectoralis insertion on the humerus is strengthened by extending its area distally down the shaft toward the radial fossa (much reduced in monachine seals) and the distal articulation. The anterior margin of the monachine humerus is, therefore, straight or even convex, and muscle scars are prominent where the deltoid crest blends distally into the shaft. A similar elongation of the pectoral insertion is also present in the otarioid

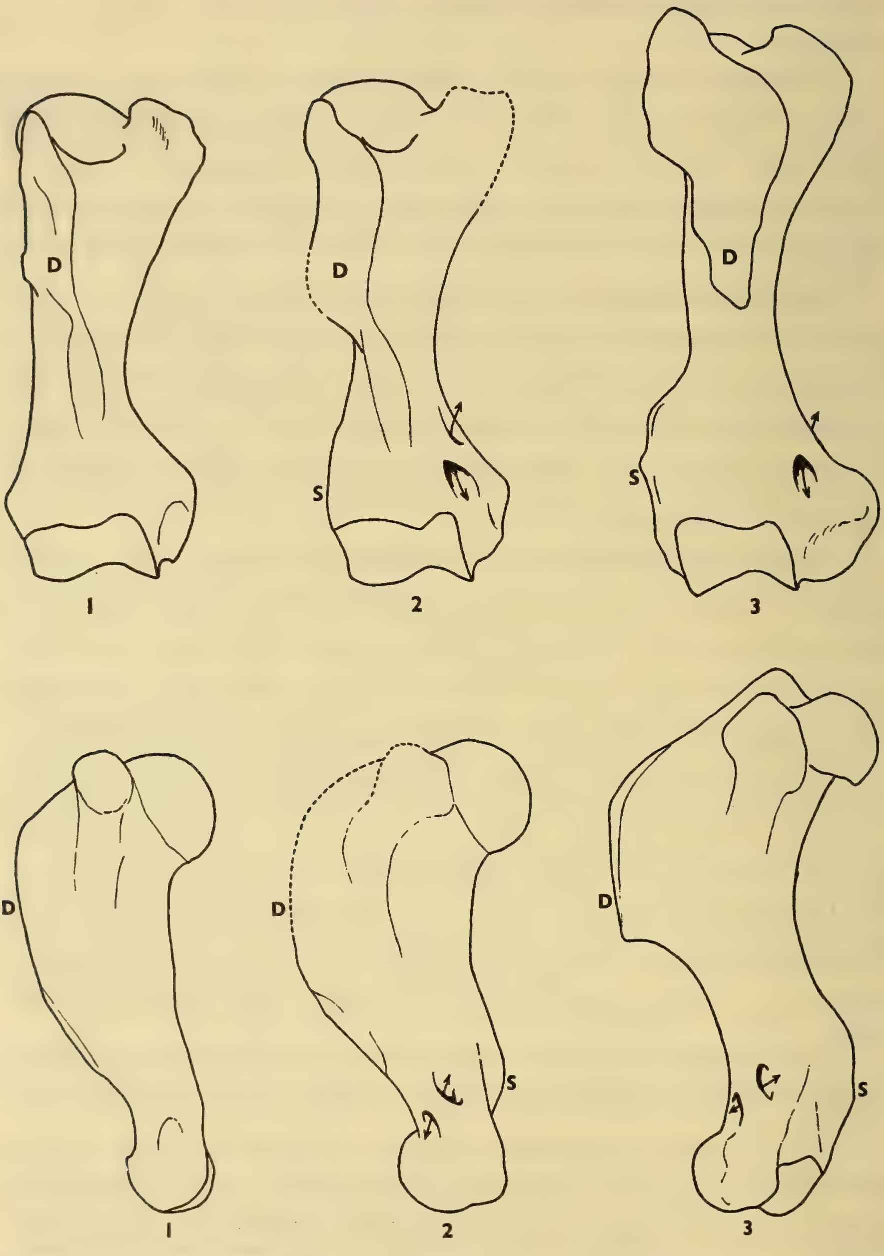

Fig. 2. Anterior and medial views of the right humeri of *Monachus schauinslandi* (1), *Prionodelphis capensis* (2), and *Erignathus barbatus* (3). (D – deltoid crest; S – supinator ridge.)

seals, consistent with the greater development of the pectoral muscles in that group.

In the *P. capensis* humerus, the bicipital or intertubercular groove is widely open, the deltoid crest blends smoothly into the distal part of the shaft, and the muscle scars are prominent on the shaft below the deltoid crest. In these respects it is typically monachine. It does, however, have the lateral overhanging of the deltoid crest similar to that of the phocines. The deltoid crest is as a result, more prominently developed than in modern monachines.

It is concluded that the pattern of strengthening of the pectoral muscle insertion is a more useful character in classifying phocids than the two characters given by King (1966), which apply to modern species only. In the *P. capensis* humerus the loss of the entepicondylar foramen, a reduction in the size of the supinator ridge and reduction of the lateral development of the deltoid crest, would reduce it to an almost exact replica of that of *M. schauinslandi.*

The humerus of *P. capensis* is stoutly proportioned, and the most complete specimen known (L 4638) has a total length of 138 mm between the head and median condyle. The transverse diameter of the distal end is 52,7 mm (mean of 8 specimens). It is stouter than that of living *Monachus* and *Leptonychotes*, and some fossil monachines such as *Pliophoca etrusca* and *Monotherium aberratum*; comparable in stoutness to the humerus of living *Hydrurga* and fossil *Palaeophoca nystii*; it is less stout than that of living *Lobodon* and *Ommatophoca.* Relatively shorter and stouter humeri suggest more pelagic adaptations in living phocids.

Ulna

According to King (1966:390) there are no consistent differences between the ulnae of phocines and monachines. In our sample of ulnae from living species there is a suggestion that the tuberosity for insertion of the internal anconeal muscle (Howell, 1929:75) is much more produced and somewhat more posterior in location in the phocine seals. In the monachine seals, if any anconeal tuberosity can be said to exist, it is continous with the triceps insertion at the anterodorsal apex of the olecranon (ulnar orientation is here considered to be with the long axis vertical, as in fissiped carnivores). There also appears to be slight but persistent sigmoid flexure of the phocine ulnar shaft, in anterior or humeral aspect, because of a lateral curve distal to the radial notch, whereas the shaft of modern monachine seals is straight distal to the radial notch.

Of these two suggestive characters, the nature of the anconeal insertion is not preserved on the ulnae of *P. capensis*, but there appears to be a slight phocine outward curvature of the shaft in the vicinity of the interosseous crest, distal to the radial notch. It thus seems possible that the straight shaft of the living monachine seals has been recently acquired.

Except for the slight curvature of the shaft, the ulna of *P. capensis* (Plate 13) greatly resembles that of *M. schauinslandi.* The proportions are nearly equal and both are characterized by an extremely elongated posterior process of the olecranon, giving the bone a very hatchet-like appearance.

There is considerable generic variation, and no subfamilial differentiation, in the configuation and relative location of the humeral and proximal radial articulation on the phocid ulna. In these articular facets *P. capensis* also resembles living *Monachus*. The radial facet has minimal medial offset and distal separation from the facet for the humerus, and faces anteriorly rather than anterolaterally as in other phocids. The humeral facet has a distinct medial curvature, as does that of many other phocids. It also seems possible, therefore, that the lateral positioning of the head of the radius, as reflected in its articulation with the ulna, may be a rather recent development, at least in the monachine seals.

The total length of the ulna of *P. capensis*, estimated from two incomplete specimens, is about 170 mm.

Radius

Reflecting the more anterior orientation of the radial articulation of the ulna, the radius of *Prionodelphis capensis* (Plate 14) was orientated more anteriorly from the ulna than is that of some living monachines and apparently all living phocines. As a result, the radial tuberosity lies distinctly on the medial side of the radius, as on the radius of living *Monachus*, and not on the posteromedial surface as is the case of the radius of living phocines.

King (1969: fig. 31) has pointed out that the distal articulations of the radii of *Hydrurga* and *Ommatophoca* have convex surfaces that curve on to the medial (flexor) side of the radius at or near the anterior (preaxial) limit of the articular surface. The radius of *Halichoerus* has this medially curving segment of the articulation about midway between the anterior and posterior limits of the articular surface. The condition in the latter produces a moderate indentation in the medial margin of the articular facet when viewed distally.

The pattern of distal articulation on the radius of *Halichoerus* seems to be a characteristic of all extant Phocinae. The radii of living monachine seals follow the patterns shown by King (1969) for *Ommatophoca* and *Hydrurga*. In *Ommatophoca* and *Mirounga* the distal articular surface is roughly rectangular, and the anteromedial quarter curves on to the medial surface. In *Hydrurga*, *Lobodon* and *Monachus* the anteromedial corner of the articulation is extended so that the part of the surface that curves on to the medial side of the radius is almost a separate articulation (see King, 1969: fig. 31b).

In *Prionodelphis capensis* the distal articulation of the radius (L 2935) most resembles that of *Mirounga*. In general configuration the radius is markedly spatulate with a prominent anterior crest for insertion of supinator and pronator teres muscles, most closely resembling in this respect, *Hydrurga* and *Ommatophoca* of the living monachines.

The total length of the radius of *P. capensis*, estimated from two incomplete specimens, is about 145 mm with the greatest anteroposterior diameter of the shaft being 51,4 mm. The dimensions of the proximal end are 30,8 by 23,4 mm (mean of seven specimens).

Posterior Limb

Innominate

The most complete innominate known (L 15849A) lacks the most anterior part of the ilium, and the posterior parts of the ischium and pubis (Plate 15). There is, however, sufficient of this bone remaining to enable a fairly confident assessment of its characteristics.

The ilium is weakly everted, approximately to the extent of that of *Erignathus* and most monachine seals. *Erignathus* is atypical of the Phocinae, the remainder of which have a strongly everted ilium 'with a deep lateral excavation' (King, 1969:392); the latter character is absent in *P. capensis*.

Comparison of the post-acetabular proportions of the entire innominate is precluded by the incompleteness of the specimens. However, a comparison of the distance between the centre of the acetabulum and the apex of the ischiatic spine, to the width of the obturator foramen ventral to the ischiatic spine (not always maximum width), results in an equally distinct separation between monachine and phocine seals (Table 5). Interestingly, measurements of photographs and drawings published by King (1956, 1966, 1969), also conform quite well.

TABLE 5. Innominate proportions of some phocids.

Species	A = Acetabulum center to tip of ischiatic spine	O = Width of obturator foramen ventral to ischiatic spine	O/A × 100
Monachus m.[1]	37,1	18,3	49,3
Prionodelphis capensis	90,8	39,8	43,8
Hydrurga l.	132,8	57,8	43,5
Hydrurga l.[2]	25,6	9,9	38,7
Leptonychotes w.[2]	24,0	9,5	39,6
Leptonychotes w.[1]	44,4	15,9	35,8
Monachus s.	95,6	36,5	38,2
Ommatophoca r.[2]	22,5	8,2	36,4
Lobodon c.	95,0	33,4	35,2
Cystophora c.	132,8	44,4	33,4
Pagophilus g.	93,8	30,3	32,3
Halichoerus g.[2]	23,3	6,9	29,6
Halichoerus g.[1]	34,9	9,4	26,9
Phoca v.	97,9	28,6	29,2
Erignathus b.	141,2	39,1	27,7
Erignathus b.[2]	28,5	7,7	27,0

[1] From photo in King, 1956.

[2] From drawing in either King, 1966, or King, 1969.

As with the living Antarctic monachines (but not *Monachus schauinslandi*) and some phocine seals, the innominate of *P. capensis* appears rather thick across the acetabulum. It appears similarly thick in available specimens of *Pagophilus* and *Cystophora*. This appearance is caused by a relatively small acetabulum.

Femur

Only the distal end of the femur of *P. capensis* is known (L 10131) (Plate 16A). The patellar facet is somewhat broader than tall, as in the monachine seals, while a fairly marked pit for the popliteus muscle on the lateral epicondyle shows resemblance to the phocine seals.

Tibia

The tibia of *P. capensis* is remarkable for the development of pronounced fossae on the posterior and antero-lateral surfaces. In the specimen L 10128/9 (Plate 16B, C, D) the thickness of bone between these two fossae is as low as 0,75 mm. This condition most resembles that in the tibia of *Halichoerus*. King (1966) states that the post-tibial fossa is more pronounced in the Phocinae than in the Monachinae.

Distally, the tibia of *P. capensis* is conspicuously broad and anteroposteriorly flattened (Plate 16E, F), a condition very similar to *Pliophoca etrusca* (Tavani, 1942: fig. 18). The fibular contact is sharply angled outward suggesting that the fibula was rather markedly bowed.

Pes

A calcaneum (L 10118), two astragali (L 10130, L 10993), one navicular (L 15851), one entocuneiform (L 10124), one metatarsal V (L 10996) and two phalanges (L 10999, L 10205) of *Prionodelphis capensis* are known (Plates 17 & 18). At first glance it seems obvious that *P. capensis* has long metatarsal bones relative to the size of the astragalus, and in fact, a sampling of the relative sizes of these two bones in seven living genera seems to bear this out (Table 6). The Langebaanweg seal appears to have relatively longer metatarsals than those of the compared living genera except *Monachus*.

TABLE 6. Tarsal-metatarsal comparison of some phocids.

Genus	(1) Greatest length of MT V	(2) Greatest length of astragalus	(3) Greatest length of cuboid-MT IV facet	(2/1)	(3/1)
Phoca	70,7 mm	59,7 mm	28,2 mm	0,84	0,398
Lobodon	98,2	75,0	35,2	0,76	0,358
Cystophora	94,6	69,9	32,4	0,74	0,342
Mirounga	129,5	90,5	47,8	0,70	(0,369)
Hydrurga	120,2	82,0	40,8	0,68	0,339
Pagophilus	85,6	57,7	25,9	0,67	(0,302)
P. capensis	89,5	57,5	30,4	0,64	0,339
Monachus	98,0	56,3	30,2	0,57	0,308

As the fossil astragali and metatarsal V were not found in association, they could represent different sized individuals, creating a false impression of relative metatarsal size. To check this possible error a similar comparison of the cuboid-metatarsal IV articular facet on metatarsal V, to the total length of the

the metatarsal was also made (Table 6). Comparable results were achieved, except for *Mirounga* and *Pagophilus* whose relative proportions were not consistent. It therefore appears probable that *P. capensis* did indeed have relatively elongated metatarsal bones and hence had relatively large hind flippers.

King (1966:393–394) has suggested that the more distal articular facet between the astragalus and the calcaneum is relatively long in the phocine seals and short in the monachines. Although there is no exception in the monachine specimens available, there seems to be great variation in the form of this facet on the astragalus of the phocine seals. Our specimen of *Cystophora* appears decidedly 'monachine' in this character: astragali of *Erignathus* appear to vary from distinctly 'monachine' to distinctly 'phocine'. This articular surface on *P. capensis* is distinctly elongated and hence 'phocine' to the extent that the character is valid.

In all respects other than their mutual lower articulation, the astragalus and calcaneum of *P. capensis* are extremely similar to those of *M. schauinslandi*. If the tibial articulation of the astragalus is arbitrarily taken to be dorsal, so that the fibular articulation is vertical, these surfaces are low relative to the body of the astragalus and the fibular articulation extends about to the most ventral limit of the bone. Among living monachines a similar condition is found in both *Monachus* and *Mirounga*, which differ greatly in this respect from *Hydrurga*. Wide variation is found also in the phocine seals: the astragalus of *Pagophilus* is perhaps most similar to that of *P. capensis*, while that of *Phoca* differs the most.

The tibial articulation is cylindrical, as in *Mirounga*, *Monachus* and *Lobodon*, rather than spherical as in *Hydrurga*. No angular boundary separates the distal articulation for the navicular from the adjacent articulation for the calcaneum. The astragalus is rather short-necked and has a short calcanear process.

The dimensions of the calcaneum L 10118 (Table 7) are remarkably similar to that of a *M. schauinslandi* specimen recorded by Robinette & Stains (1970: table 1), while its porportions are clearly monachine rather than phocine (Robinette & Stains, 1970: table 2). The metrical data presented in Table 7 confirms the observations on the similarities between the calcanea of *P. capensis*, *Monachus* (especially *M. schauinslandi* and *M. tropicalis*) and *Mirounga*, and also illustrates differences from those of *Hydrurga*, *Leptonychotes* and *Ommatophoca*.

The posterior[1] astragalar articulation of the calcaneum of *P. capensis* is narrow relative to its length. This contrasts with that facet of the calcaneum of *Hydrurga* and *Monachus schauinslandi*, in which it is nearly as wide as it is long. Robinette and Stains (1970:535) state that the facet is narrower on the calcaneum of *M. tropicalis* than on that of *M. schauinslandi*.

The facet of the navicular, for articulation with the entocuneiform, is notably equidimensional and flat. The articular surface on the entocuneiform, for contact with metatarsal I, is notably elongated, suggesting a more slotted

---

[1] As used by Robinette & Stains (1970: fig. 1); this is the anterior articulation of King (1966: 393).

TABLE 7. Dimensions of calcaneum of *Prionodelphis capensis* from Langebaanweg, compared with those of some modern monachines.

Species	N	TL	W	DVH	W/TL	DVH/TL	DVH/W
Monachus monachus†	1	63,2	29,8	30,0	47	47	101
Mirounga angustirostris†	6	79,0*	40,9*	38,7*	52	49	95
Monachus schauinslandi†	1	59,1	31,9	30,3	54	51	95
Monachus tropicalis†	1	54,9	27,3	28,5	50	51	104
Prionodelphis capensis	1	58,4	30,7	30,4	53	52	99
Hydrurga leptonyx†	1	74,5	38,7	42,0	52	56	108
Leptonychotes weddelli†	1	71,5	38,2	41,9	53	58	110
Ommatophoca rossi†	1	56,0	30,4	34,6	54	61	114

† From Robinette & Stains, 1970.
TL = total length.
DVH = dorsoventral height.
* Average figures.
W = width.

proximal articulation rather than the basined articulation on metatarsal I of most living seals. Although both the navicular and the entocuneiform appear large relative to the known astragali and calcaneum, they appear to be undiagnostic of subfamily affinities.

As has been mentioned, metatarsal V appears to be relatively elongated. The two known phalanges also appear to be conspicuously elongated and slender when compared with those of living phocids. Otherwise they seem to have no distinctive features.

DISCUSSION

In assigning the Langebaanweg phocid to the genus *Prionodelphis*, it is recognized that reassessment may be required when more material of *P. rovereti* is found. Generic identity is based upon the remarkable similarity of the few fragments from Argentina to the South African material and on the belief that the lack of greater knowledge is a stronger argument against the establishment of a new genus than it is against tentative assignment to the same genus.

The similarity of the cheek teeth of *P. rovereti* and *P. capensis* is very strong. The transverse narrowness of the cheek-teeth, more evident in the latter species, and a posterointernal shelf on the upper cingula only, are features found only in some of the Antarctic genera of the monachine seals. As mentioned, the tooth proportions and cingular shelf are most similar to the condition in *Hydrurga*. In addition, the greatly reduced and distinctly recurved last upper postcanine, of both species of *Prionodelphis* is singularly suggestive of a close relationship, and is not known in other monachine seals, although there is some resemblance to the more anterior cheek teeth of *Leptonychotes*, and to a lesser extent also *Ommatophoca*.

Apart from differences in the dimensions of the teeth of *P. capensis* and *P. rovereti*, some differences in morphology are also evident. Other than the upper fifth, the only known upper postcanine of *P. rovereti* (Frenguelli, 1922: fig. 1), differs from the second to fourth upper postcanines of *P. capensis* in having a far larger posterior root, which is at least partially divided longitudinally. This feature of the Argentinian species, as well as its slightly broader cheek-teeth, can be interpreted as being less advanced characteristics. The anterior part of the crown of this tooth of *P. rovereti* lacks a distinct accessory cusp, which is present in all the known postcanines of *P. capensis.* The anterior part of the *P. rovereti* tooth is markedly convex, and the lingual view (Frenguelli, 1922: fig. 1c) shows a small step more or less where an accessory cusp might be expected. It is possible, therefore, that this specimen has the anterior accessory cusp masked by some individual variation, and that normally such a cusp was present. The lower postcanines of *P. rovereti* (Frenguelli, 1922: fig. 2B, C) are illustrated as having not one, but two anterior accessory cusps, with the anterior and posterior parts of the teeth being almost mirror images of one another. In none of the postcanines of *P. capensis* is a second anterior accessory cusp known, and its development in the Argentinian species could be a more advanced specialization.

The age of the Argentinian species is even more uncertain than that from Langebaanweg. The Entre Rios deposits, from which the specimens of *P. rovereti* came, appear to be of Pliocene age (Langston, 1965: table 3) and would seem, therefore, to be roughly the same age as those from Langebaanweg. However, most often these deposits have been referred to as being late Miocene or early Pliocene, and the latter age is given by Romer (1966).

Discussion on the relationship of *P. capensis* to *P. rovereti* will be more meaningful when more specimens of the latter are known, but the observed differences between the two sets of specimens, the possibility of a temporal difference in the deposits from which they come, and their geographical separation suggest a distinction between the South African and Argentinian fossils at least at the species level.

The relatively poor fossil record of the Phocidae in general renders interpretation of the wider relationships of *P. capensis* equally problematical. Some features of the fossil seal from South Africa are found, among the living seals, only in the Phocinae. However, a number of features are clearly monachine and these suggest that the dichotomy from the primitive phocid into the two extant subfamilies was a result of two distinctly different patterns of specialization to better adapt to pelagic existence. These adaptations relate to, amongst other things, greater swimming ability and underwater hearing. As has been pointed out throughout the description, in all of these adaptations *P. capensis* has clearly followed the monachine pattern.

To judge from the comparisons between *P. capensis* and the living phocine and monachine seals, differences in adaptation toward greater swimming ability appear most evident in the proximal limb elements. Subfamilial differences in the structure of the humerus related to the strengthening of the pectoralis muscle have been outlined in the discussion of this bone. In the Phocinae the pectoralis insertion has been strengthened by exaggeration of the deltoid crest, and in the Monachinae strengthening of this same muscle has been accompanied by a distally extended insertional area on the humerus shaft.

One might infer that the phocid ancestral to the living subfamilies had a humerus of relatively slender proportions showing a moderate development of both types of pectoralis insertion, such as seen on the humerus of '*Phoca*' *vindobonensis* Toula (1897: pl. 1, fig. 16) or *Leptophoca lenis* True (1906: pl. 75). Such fossil phocids as *Monotherium aberratum* Van Beneden (1877: pl. 17, figs. 1–4) appear to have the insertional area extended so far distally on the shaft that a monachine condition seems indisputable, while others such as *Phocanella pumila* Van Beneden (1877: pl. 14, figs. 1–4), have clearly evolved the phocine condition by strengthening the deltoid crest and eliminating all pectoralis insertion on the shaft distal to the crest. In addition, the presence of an entepicondylar foramen on the humerus appears to be a primitive feature. It is present in all of these fossil seals, including *Prionodelphis capensis*, and is retained in the living phocine seals as well. Only at the stage of evolution evident in the living phocids does the presence of this foramen become diagnostic of subfamily affinity.

Consideration of the subfamilial differences in swimming adaptations which might be found in the pelvic limbs has been hampered in this study by the lack of a complete specimen of the femur of *P. capensis*. Nevertheless, King (1966:392) has pointed out that, except for the genus *Erignathus*, the phocine seals may be recognized by their extremely everted ilium. Both leverage and strength of the insertion of the massive muscles of the back, the iliocostalis system, are benefited by this structure, as well as are most of the gluteus group which directly transfers the forces of the back to the femur to produce the characteristic phocid swimming motion. The advantages of this structure seem so obvious that it is puzzling why none of the monachine seals have developed it, or why it developed so late in the history of the phocid seals. Few fossil seals in which the pelvis is known, exhibit the phocine everted ilium.

The interpretation of the functions of osteological characters in the phocine and monachine ear regions is subjective, but according to one interpretation (Repenning, in press), two of these differences relate to improved underwater hearing.

The presence of a more or less horizontal crest on the external surface of the mastoid bone in all phocine seals is correlated with a greater directional selectivity of sounds in water originating above or below the head; this crest is not present in the monachine seals, including *P. capensis*.

The development of an enlarged petrosal apex in all seals is correlated with a greater sensitivity to sound in water, and this development is conspicuously less in *P. capensis* than in the living Antarctic seals. The enlargement of the petrosal apex is in the form of a globular mass in the phocine seals, while in the monachine seals, with the exception of *Mirounga*, the apex is enlarged as a rather low and broad structure. In this respect *P. capensis* is clearly monachine.

It should also be noted that broadening is slight in *Hydrurga*, and that enlargement of the apex is partly accomplished by thickening; the structure does not appear globular as in the phocine seals, however. Furthermore, enlargement of a petrosal apex is minimal in *Monachus*, less than in *P. capensis;* in this respect *Monachus* might be expected to be most similar to the ancestral phocid from which the extant subfamilies evolved.

Monachus is the least specialized of the living monachine seals in the enlargement of the petrosal apex, strengthening of the humerus, distal broadening of the radius, enlargement of the ilium, strengthening of the femur and modification of the dentition. Except for the condition of the femur, which is unknown in the South African fossil, and possibly the enlargement of the ilium, which is incompletely preserved, *Monachus* is also less specialized in these features than *P. capensis*.

From the preceding consideration of *Prionodelphis capensis* and related seals, the following features appear most likely to be those that would characterize the ancestral protophocid from which the two modern subfamilies, the Phocinae and the Monachinae, evolved: dentition with primary cusp flanked by one accessory cusp anteriorly and one posteriorly, much the same as seen in *Praepusa pannonica* Kretzoi (1941: fig. 1), ear region much as in living *Monachus*, and postcranial skeleton unspecialized as in '*Phoca*' *vindobonensis* Toula (1897).

The relationship of *P. capensis* to the Antarctic monachines is evident in a broad sense, but it is not clearly ancestral to any of the four living genera. The highly modified dentitions of the living genera differentiate them most strikingly from the Pliocene fossil. The great reduction of the last upper postcanine tooth of *P. capensis* seems to preclude the possibility of it being ancestral to *Hydrurga* or *Lobodon*, while the great simplification of the teeth of *Leptonychotes* and *Ommatophoca* leave little basis for interpretation. *Hydrurga*, *Lobodon* and *Ommatophoca* are all clearly better adapted to pelagic life in their postcranial specializations than was *P. capensis*. All of the Antarctic seals, and *Leptonychotes* in particular, have a greater development of the petrosal apex than does *P. capensis*, which indicates that the latter had less acute hearing underwater. In all these respects *P. capensis* is less advanced than the Antarctic seals, but more advanced than *Monachus*.

It seems probable that *Prionodelphis*, presently known only by the species *P. rovereti* and *P. capensis*, was not the only Pliocene monachine of the southern seas, and that some or all of the modern Antarctic genera derive from a related but unknown form.

All previously described fossil phocids are known from incomplete remains and a good many from a very few, or even one bone. The humeri and femora are the most commonly described because they are among the more durable bones of the body, and, presumably, their size lends them to discovery. Excluding mandibular fragments, *Pliophoca etrusca* Tavani (1942; a skull), *Phoca pontica* Eichwald (1853; a cranium) and *Phoca pontica* Alekseev (1924; a rostrum) are the only fossil phocids of which the skulls are even partially known. Despite its fragmentary nature, *Prionodelphis capensis* is one of the most completely known fossil phocids, and since the systematic investigation of the Langebaanweg deposits is still in its early stages, it can be expected that much more material will become available for study in the future.

SUMMARY

Pinniped remains from the late Pliocene deposits at Langebaanweg in South Africa are described. The material is referred to *Prionodelphis capensis* n. sp. (family Phocidae, subfamily Monachinae). On the basis of this material, the genus *Prionodelphis* Frenguelli 1922 is defined. The relationships of the Langebaanweg species to extant and fossil monachines are discussed, and morphological characters, by which fossil Phocinae and Monachinae can be differentiated are suggested.

ACKNOWLEDGEMENTS

We wish to thank A. W. Mansfield and D. E. Sergeant of the Fisheries Research Board of Canada; C. W. Mack of the Harvard University Museum of Comparative Zoology; O. P. Pearson and R. L. Jones of the University of California Museum of Vertebrate Zoology; R. H. Mansville, K. W. Kenyon, and E. Kridler of the (U.S.) Bureau of Sport Fisheries and Wildlife; C. O. Handley, Jr. and C. E. Ray of the (U.S.) National Museum of Natural History; E. H. Bryan, Jr. of the Bernice P. Bishop Museum (Honolulu); F. H. Fay of the (U.S.) Arctic Health Research Center; and L. Giannelli of the Universita di Pisa Museo di Paleontologia for the loan or gift of material used in this study.

The current investigations at Langebaanweg are being supported by the South African Council for Scientific and Industrial Research, Chemfos Ltd. (a subsidiary of the African Metals Corporation) and Shell South Africa (Pty.) Ltd. The Wenner-Gren Foundation for Anthropological Research, New York, provided the vehicle used in the field work at Langebaanweg (Grant no. 2752–1834).

We are indebted to Mr. H. Krumm and Mr. G. Benfield of Langebaanweg, whose co-operation with the South African Museum led to the recovery of most of the material described in this paper.

Francis H. Fay and Clayton E. Ray kindly offered comments on the manuscript of this paper, and we are grateful to them for their observations and criticisms.

REFERENCES

ALEKSEEV, A. K. 1924. [Seals in the Sarmatian deposits of southern Russia.] *Zh. nauchno-issled. Kafedr Odesse* **1**: 26–34. [In Russian.]

ALLEN, J. A. 1880. History of North American pinnipeds: a monograph of the walruses, sea-lions, sea-bears and seals of North America. *Misc. Publs U.S. geol. geogr. Surv. Territ.* **12**: i–xvi, 1–785.

BONÉ, E. L. & SINGER, R. 1965. *Hipparion* from Langebaanweg, Cape Province, and a revision of the genus in Africa. *Ann. S. Afr. Mus.* **48**: 273–397.

Brookes, J. 1828. *A catalogue of the anatomical and zoological museum of Joshua Brookes*. London.

Burns, J. J. & Fay, F. H. 1970. Comparative morphology of the skull of the Ribbon seal, *Histriophoca fasciata*, with remarks on systematics of Phocidae. *J. Zool.* **161**: 363–394.

Cabrera, A. 1926. Cetáceos fósiles del Museo de La Plata. *Revta Mus. La Plata.* **29**: 363–411.

Eichwald, C. E. von. 1853. *Lethaea Rossica, ou Paleontologie de la Russie.* **3**: Stuttgart: Schweizerbart.

Frenguelli, J. 1922. *Prionodelphis rovereti* un representante de la familia 'Squalodontidae' en al Paranense Superior de Entre Rios. *Boln Acad. nac. Cienc. Córdoba* **25**: 491–500.

Frenguelli, J. 1926. El Entrerriense de Golfo Nuevo en el Chubut. *Boln Acad. nac. Cienc. Córdoba* **29**: 191–270.

Gray, J. E. 1825. An outline of an attempt at the disposition of Mammalia into tribes and families, with a list of the genera apparently appertaining to each tribe. *Ann. Philosophy* (n.s.) **10**: 337–344.

Hay, O. P. 1930. Pinnipedia. *In* hay, o. p. *Second bibliography and catalogue of the fossil Vertebrata of North America.* **2**: 555–565. Washington: Carnegie Institution. (*Publs Carnegie Instn* 390.)

Hendey, Q. B. 1970*a*. A review of the geology and palaeontology of the Plio/Pleistocene deposits at Langebaanweg, Cape Province. *Ann. S. Afr. Mus.* **56**: 75–117.

Hendey, Q. B. 1970*b*. The age of the fossiliferous deposits at Langebaanweg, Cape Province. *Ann. S. Afr. Mus.* **56**: 119–131.

Howell, A. B. 1929. Contribution to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). *Proc. U.S. natn. Mus.* **73**: 1–142.

Illiger, C. 1811. *Prodromus systematis mammalium et avium.* Berlin: Salfeld.

Kellogg, R. 1922. Pinnipeds from Miocene and Pleistocene deposits of California. *Univ. Calif. Publs geol. Sci.* **13**: 23–132.

Kellogg, R. 1942. Tertiary, Quaternary, and Recent marine mammals of South America and the West Indies. *Proc. 8th Am. Sci. Congr.* (Washington) **3**: 445–473.

King, J. E. 1956. The monk seals (genus *Monachus*). *Bull. Br. Mus. nat. Hist.* (Zool.) **3**: 201–256.

King, J. E. 1964. *Seals of the world.* London: British Museum (Natural History).

King, J. E. 1966. Relationships of the Hooded and Elephant seals (genera *Cystophora* and *Mirounga*). *J. Zool.* **148**: 385–398.

King, J. E. 1969. Some aspects of the anatomy of the Ross seal, *Ommatophoca rossi* (Pinnipedia: Phocidae). *Scient. Rep. Br. Antarct. Surv.* **63**: 1–54.

Kraglievich, L. 1934. La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal. *Siglo ilustrado, Montevideo* **938**: 1–136.

Kretzoi, M. 1941. Seehund-Reste aus dem Sarmat von Erd bei Budapest. *Földt. Közl.* **71**: 350–356.

Langston, W. 1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *Univ. Calif. Publs geol. Sci.* **52**: i–vii, 1–157.

Maglio, V. J. & Hendey, Q. B. 1970. New evidence relating to the supposed stegolophodont ancestry of the Elephantidae. *S. Afr. archaeol. Bull.* **25**: 85–87.

Mckenna, M. 1969. The origin and early differentiation of therian mammals. *Ann. N.Y. Acad. Sci.* **167**: 217–240.

Repenning, C. A. Underwater hearing in seals: functional morphology. *In Functional anatomy of marine mammals.* London: Academic Press. (In press.)

Robinette, H. R. & Stains, H. J. 1970. Comparative study of the calcanea of the Pinnipedia. *J. Mammal.* **51**: 527–541.

Romer, A. S. 1966. *Vertebrate paleontology.* 3rd ed. Chicago: University Press.

Savage, D. E. & Curtis, G. H. 1970. The Villafranchian stage-age and its radiometric dating. *Spec. Pap. geol. Soc. Am.* **124**: 207–231.

Scheffer, V. B. 1958. *Seals, sea lions and walruses.* Stanford: University Press.

Singer, R. & Hooijer, D. A. 1958. A *Stegolophodon* from South Africa. *Nature, Lond.* **182**: 101–102.

Smirnov, N. A. 1908. [Review of Russian pinnipeds.] *Mém. Acad. Sci. St. Petersb.* (8) **23**: 1–75. [In Russian].

Tavani, G. 1942. Revisione dei resti del pinnipede conservato nel Museo di Geologia di Pisa. *Palaeontogr. ital.* **40**: 97–113.

Tavani, G. 1943. Revisione dei resti di pinnipedi conservati nel Museo geo-paleontologico di Firenze. *Atti. Soc. tosc. Sci. nat.* Memorie **61**: 34–42.

Toula, F. 1897. *Phoca vindobonensis* n. sp., von Nussdorf in Wien. *Beitr. Paläont. Geol. Öst.-Ung.* **11**: 47–70.

TROUESSART, E.-L. 1897. *Catalogus mammalium tam viventium quam fossilium.* Berlin: Friedländer.

TRUE, F. W. 1906. Description of a new genus and species of fossil seal from the Miocene of Maryland. *Proc. U.S. natn. Mus.* **30**: 835–840.

UGOLINI, R. 1902. Il *Monachus albiventer* Bodd. del Pliocene di Orciano. *Palaeontogr. ital.* **8**: 1–20.

VAN BENEDEN, P. J. 1877. Description des ossements fossiles des environs d'Anvers. *Annls Mus. r. Hist. nat. Belg.* **1**: 1–88.